TWO NEW ANOMALOCYSTITID MITRATES FROM THE LOWER DEVONIAN HUMEVALE FORMATION OF CENTRAL VICTORIA

MARCELLO RUTA AND PETER A. JELL

Ruta, M. & Jell, P.A. 1999 06 30: Two new anomalocystitid mitrates from the Lower Devonian Humevale Formation of central Victoria. *Memoirs of the Queensland Museum* **43**(1): 399-422. Brisbane. ISSN 0079-8835.

The anomalocystitid mitrates *Victoriacystis holmesorum* sp. nov. and *Pseudovictoriacystis problematica* gen. et sp. nov. are described from the Lower Devonian Humevale Formation of central Victoria. *V. holmesorum* varies consistently from the type species, *V. wilkinsi*, in the size (larger), shape and proportions of some body plates, the larger more robust spines and the shape of ossicles of distal part of appendage. Some specimens have a sinuous to crook-shaped right spine; others have a proximally geniculate right spine; the left spine is more robust than the right and cigar-shaped. *Pseudovictoriacystis problematica* has an unusual plate configuration on convex surface, which consists of 14 plates, without intervening row II, apparently without C16 and C18, and with a greatly elongate C17. Otherwise it is very similar to *V. holmesorum*, especially in distribution of terrace-like ridges and shape and proportions of plates on plano-concave surface. ❒ *Anomalocystitida, Victoriacystis, Pseudovictoriacystis, Devonian, Australia.*

Marcello Ruta, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom; Peter A. Jell, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia; received 2 March 1998.

Victoriacystis was the first anomalocystitid described from Australia (Gill & Caster, 1960). The type species, *V. wilkinsi* Gill & Caster, 1960, redescribed by Ruta (1997), occurs in the lower Ludlovian of the Dargile Formation near Heathcote and the Melbourne Formation at Hawthorn, Melbourne. Although the material from the Melbourne suburb of Hawthorn has been considered Lower Silurian (Gill & Caster, 1960; Talent, 1967; Ruta, 1997), it occurs in the Melbourne Formation of Vandenberg (1988) and is thus Ludlovian. Its age is, therefore, similar to that of the specimens from Heathcote. An incomplete and poorly preserved mitrate (NMVP16880, 16881) from the Lower Devonian part of the Humevale Formation near Kinglake West was attributed by Gill & Caster (1960) to *V.* aff. *wilkinsi*. Ruta (1997) considered it inseparable from the type species. However, additional, more complete specimens from the same locality show that the Lower Devonian *Victoriacystis* is specifically distinct.

Herein, we revise the diagnosis of *Victoriacystis* (Gill & Caster, 1960; Ruta, in press), taking account of the Lower Devonian species and newly available specimens of Upper Silurian *V. wilkinsi* which are treated elsewhere (Ruta & Jell, 1999b).

A second Lower Devonian anomalocystitid mitrate genus from the Humevale Formation, known from a single, partially disrupted individual, is similar to the new species of *Victoriacystis* in the plano-concave surface, but has an unusual plating pattern on the convex surface.

GEOLOGICAL SETTING

Material described, about 30 partially to fully articulated specimens, comes from NMVPL252 (=Davies Quarry (Gill, 1948); =Middendorp's Quarry (Williams, 1964)) on the western branch of Stony Creek, about 1.6km N of Kinglake West State School and 40km NNE of Melbourne; the site is Lochkovian (Gill & Caster, 1960; Strusz, 1972; Vandenberg, 1988; Vandenberg et al., 1976; Holloway & Jell, 1983; Jell, 1983). Fossils are found in a steely grey pyritic siltstone and are concentrated in a few thin bands interspersed through about 30m exposed in the quarry wall. The diverse fossil faunas are considered to be '... pockets of organic debris ... that do not represent natural assemblages' (Jell, 1983: 210) based on disrupted bedding, attitude of various fossilised individuals and the great concentration of animals in a few thin beds.

Analysis of *Gillocystis runcinata* (ophiocistioid), *Hillocystis atracta* (rhombiferan) and *Sphagoblastus adectus* (blastoid) (Jell, 1983) suggests that the animals were probably buried when they were still alive and were flattened or slightly crushed by pressure from overlying sediment, depending upon the degree of rigidity of their thecae. Plate dislocation is minimal or does not occur at all. Almost complete absence of skeletal disruption, fractured individual plates, preservation of oral and aboral sides as internally contiguous surfaces (e.g. jaw apparatus of *Gillocystis* against inner aboral surface) and collapse of periproctal plates onto internal side of dorsal thecal surface (e.g. *Hillocystis*) indicate that sediment did not usually enter the body cavity and that geostatic compression of skeletons occurred soon after burial and before soft tissue decay.

Mode of preservation of several individuals of *V. holmesorum* is similar to that of *Sphagoblastus* but may differ from that of *Gillocystis* and *Hillocystis*. Most mitrate specimens are preserved as external moulds, often covered with thin layers of iron oxides. As in *Sphagoblastus*, the theca of *Victoriacystis* is a rigid structure composed of tightly sutured polygonal plates. In most cases, both its convex surface and its plano-concave surface are found almost completely articulated. Disruption is minimal and affects mainly LOP, MOP and C1-C9. Such plates generally lie in close proximity to each other and to the rest of the skeleton and their mutual spatial relationships are often almost unchanged.

Fractures occur usually along lateral margins of the plano- concave surface and on plates PLM, C and C20-C22 and are more numerous in the proximal 1/3 of the body, where, as in the case of other mitrates, the skeleton reaches maximum thickness and greatest curvature (Parsley, 1991). Fractures are sometimes visible at junctions between horizontal and subvertical projections of plates DLM, ILM and PLM. In these cases, subvertical projections often lie flush with convex surface plates while retaining their mutual contacts with them. In some specimens, the convex surface is collapsed onto the plano-concave surface and disruption occurs mainly at level of sutures between lateral plates of convex surface and subvertical projections of DLM, ILM and PLM. C17 is often found sutured with C16 and C18 in contrast with the situation observed in other anomalocystitids in which, when present, this plate is rarely in place (Dehm, 1932; Jefferies & Lewis, 1978; Kolata & Jollie, 1982; Parsley, 1991; Ruta, 1997; Ruta & Bartels, 1998). In a number of specimens, one or, exceptionally, both distal spines are found articulated to DLM, or at a short distance from the body. More frequently, both spines are missing.

Few specimens retain intact appendages, and even in those cases, only proximal and intermediate parts are still in place; ossicles and paired plates of distal part are not preserved. Usually, the tetramerous rings of the proximal part are complete but collapsed while retaining their telescopic arrangement. Separation of ring elements is rare as is their preservation as fully undeformed structures. In some specimens, paired plates and ossicles of the distal part are preserved intact and undeformed, albeit rarely articulated with each other. Frequently, plates are disarticulated, collapsed onto the abapical surface of ossicles or missing altogether. Sometimes, paired plates (especially proximal) are found detached from ossicles while still overlapping each other proximo-distally. The ossicles frequently maintain their alignment. Proximal and distal articular surfaces are observed in at least one individual.

Although rare and largely incomplete in their proximal 1/2, internal moulds are sometimes associated with partially disrupted external moulds. Unlike other Lower Devonian echinoderms from the Humevale Formation, *Victoriacystis* has a relatively large, transversely elongate distal orifice through which fine sediment could easily enter the body cavity during burial. Similar preservation is known in other carpoids, both solutes (Jefferies, 1990) and cornute stylophorans (Jefferies, 1968; Woods & Jefferies, 1992).

SYSTEMATIC PALAEONTOLOGY

External skeletal terminology and plate nomenclature follow Ruta (in press) with modifications as in Ruta & Jell (1999a). Description of internal body anatomy is based on Ubaghs (1968, 1969). Morphological terminology of ossicles is that of Jefferies & Lewis (1978) and Ruta & Theron (1997). The terms 'apical' and 'abapical' indicate the position of structures close to or away from the ossicular process (or apex) respectively. Specimens are deposited in the Palaeontological Collections of the National Museum of Victoria, Melbourne (NMVP) and the locality is registered in the locality register at the same Museum (NMVPL). Study and illustration of skeletal details was made on latex casts whitened with ammonium chloride.

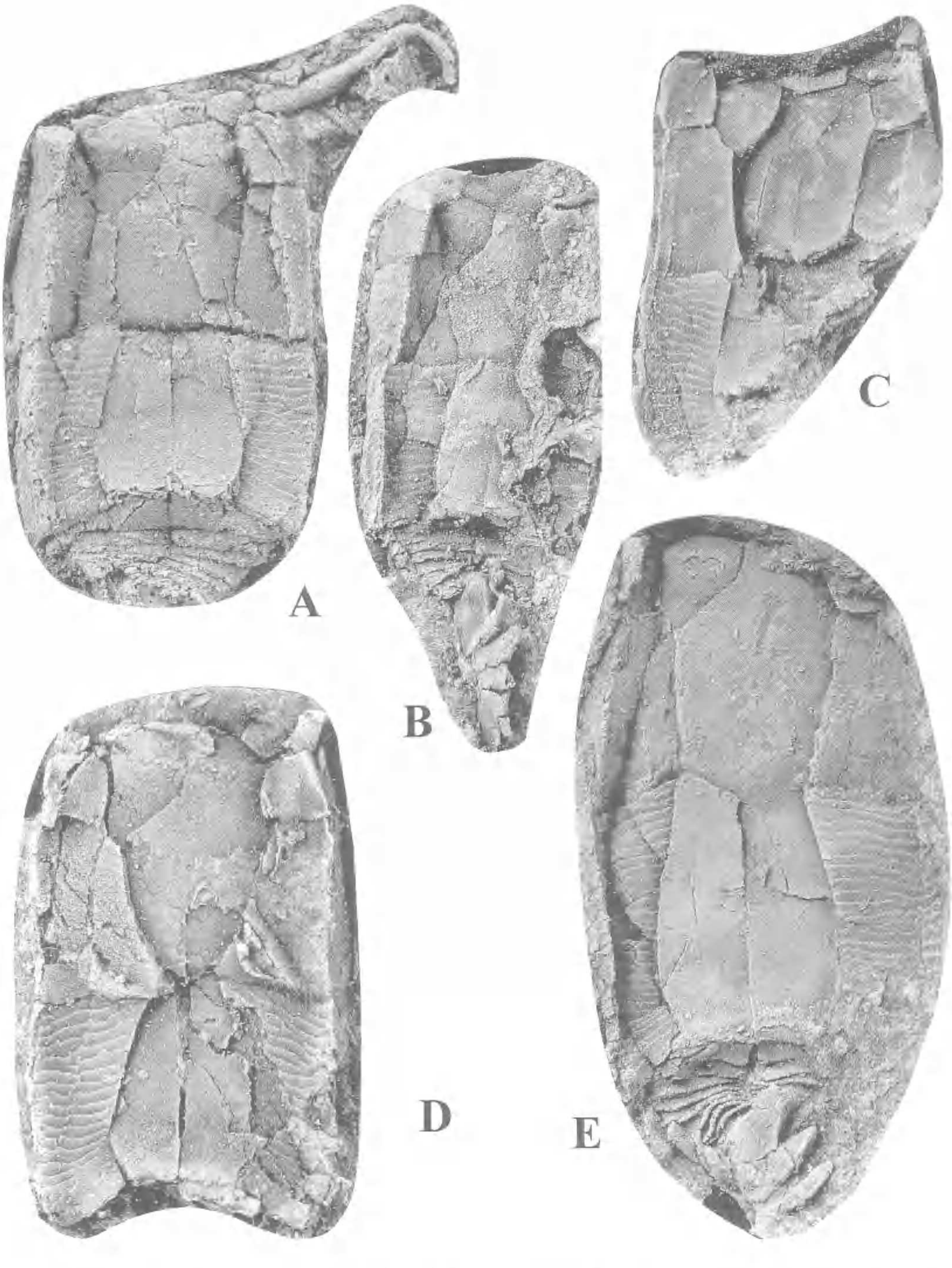

FIG. 1. *Victoriacystis holmesorum* sp. nov. All plano-concave surfaces showing terrace-like ridges, spines, tetramerous rings, styloid and proximal ossicles. A, NMVP100361. B, NMVP100387b. C, NMVP100385. D, NMVP100369. E, NMVP100373. All ×3.

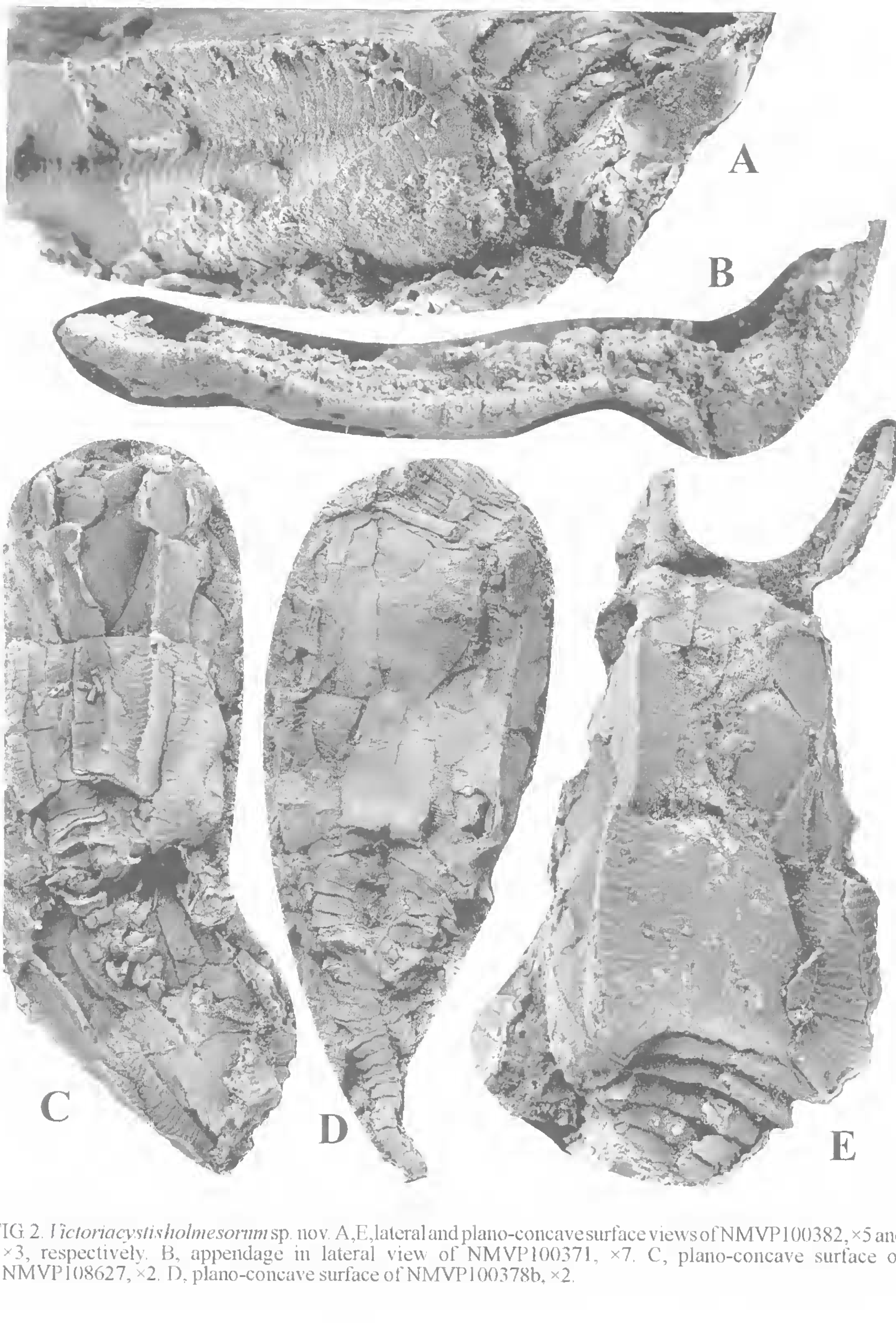

FIG. 2. *Victoriacystis holmesorum* sp. nov. A,E, lateral and plano-concave surface views of NMVP100382, ×5 and ×3, respectively. B, appendage in lateral view of NMVP100371, ×7. C, plano-concave surface of NMVP108627, ×2. D, plano-concave surface of NMVP100378b, ×2.

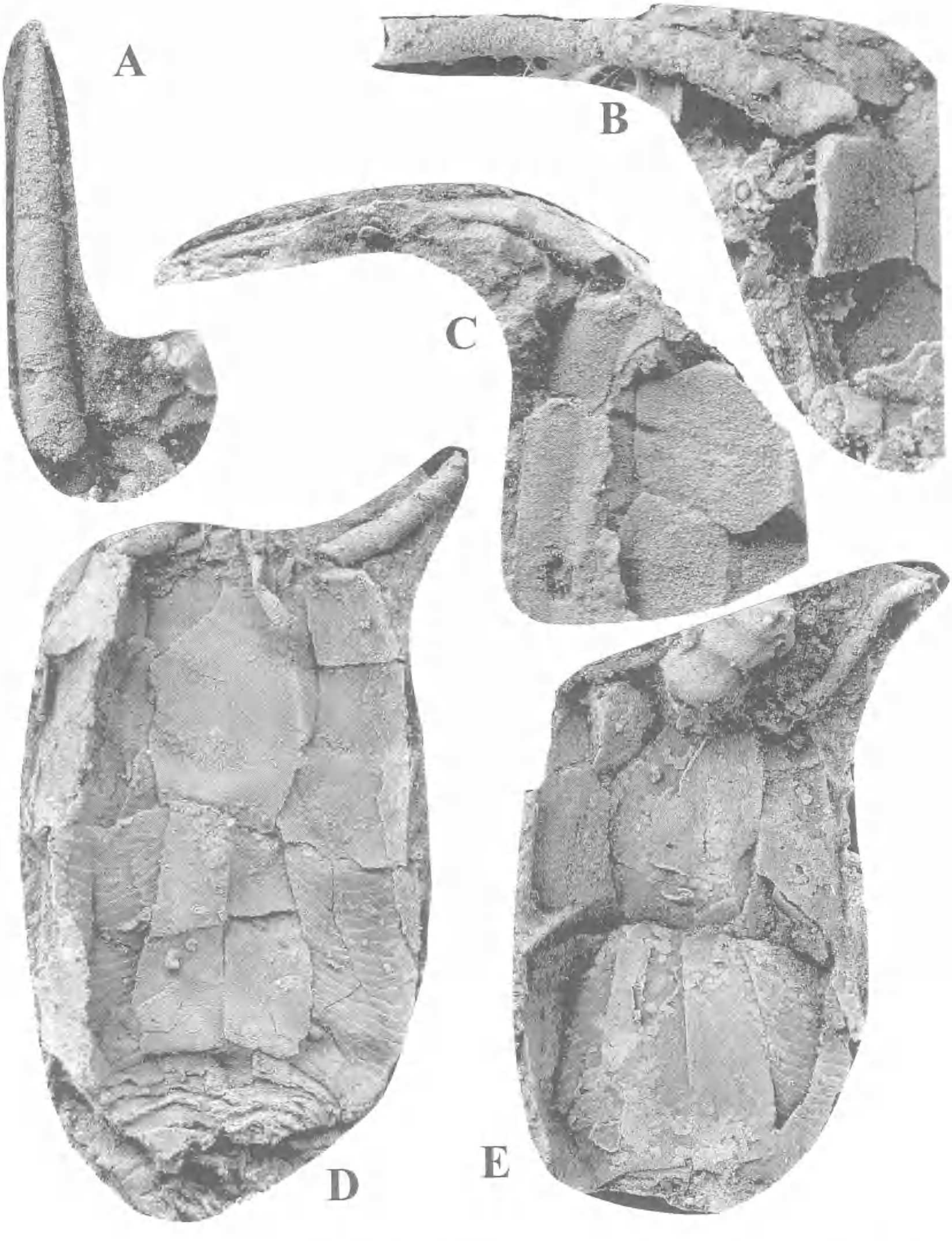

FIG. 3. *Victoriacystis holmesorum* sp. nov. A, left spine of NMVP100365, ×5. B, right spine and articulation of NMVP100371, ×7. C, right spine and articulation of NMVP100367, ×5. D, plano-concave surface of NMVP100381, ×3. E, plano-concave surface of NMVP100384, ×3.

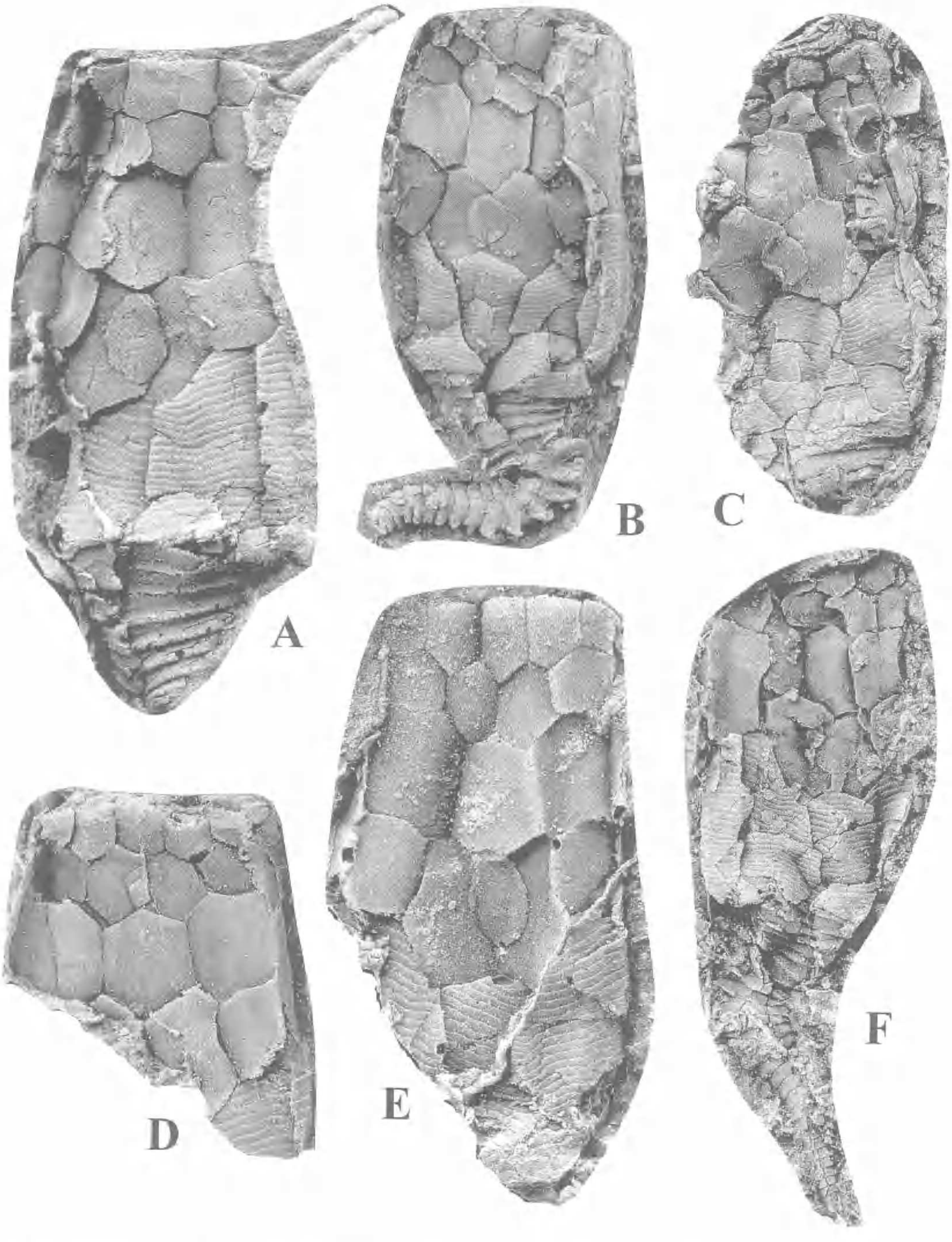

FIG. 4. *Victoriacystis holmesorum* sp. nov. All convex surfaces, showing terrace-like ridges, spines, tetramerous rings, styloid and ossicles. A, NMVP100362, ×3. B, NMVP100363 (holotype), ×2. C, (distally damaged) NMVP100378b, ×2. D, (partial)NMVP100385, ×3. E, NMVP100376, ×3. F, NMVP100374, ×2.

Superorder STYLOPHORA Gill & Caster, 1960
Order MITRATA Jaekel, 1918
Suborder ANOMALOCYSTITIDA Caster, 1952
Family PLACOCYSTITIDAE Caster, 1952

REMARKS. Family groupings in the Anomalocystitida are not satisfactory (Parsley, 1991; Ruta & Theron, 1997; Ruta, in press; Ruta & Bartels, 1998). Analysis of character distribution (Ruta, in press) suggests that, with the exception of the Allanicytidiidae Caster & Gill, 1968, all families, including Placocystitidae as defined by Parsley (1991), are not monophyletic. Parsley (1991) and Ruta (in press) concur in recognising *Victoriacystis* as sister taxon to (*Placocystites* + *Rhenocystis*). However, the allanicytidiids are not closely related to these 3 genera. As Parsley (1991:16) pointed out, their '... assignment to the Placocystitidae is admittedly speculative'. In the light of the revised family concept of Parsley (1991), we restrict this family to *Placocystites*, *Rhenocystis* and *Victoriacystis* only.

Victoriacystis Gill & Caster, 1960

TYPE SPECIES. *Victoriacystis wilkinsi* Gill & Caster, 1960 from the early Ludlow Graptolite Beds, Dargile Formation, Victoria; by original designation.

DIAGNOSIS. Rows I-V with 5,4,3,5,3 plates, respectively. C1 and C5 smaller than C2-C4. C17 elliptical to rounded, c.1/2 as long as adjacent C16 and C18. Sutures between C15 and C16 and between C18 and C19 medially convex. C21 shield-shaped to rhomboidal, deeply but not completely inserted between C20 and C22. B absent. A-C suture oblique. Robust, transverse terrace-like ridges mainly confined to C20-C22 and PLM. Lateral margins of PM convex laterally. Tetramerous rings wider proximally than distally, with fold of polyplated integument between rings. Styloid with median longitudinal keel, proximal blade elliptical in section, distal blade spine-like. Successive ossicles decreasing rapidly in size.

Victoriacystis holmesorum sp. nov.
(Figs 1-13)

Victoriacystis aff. *wilkinsi* Gill & Caster, 1960:54, pl. 10, figs 1, 3.
Victoriacystis wilkinsi Gill & Caster; Ruta, 1997:85, fig. 5A,C.

ETYMOLOGY. For Frank and Enid Holmes, for their assistance in collecting the material.

MATERIAL. HOLOTYPE: NMVP100363. PARATYPES: NMVP100361-100362, 100364-100382, 100384-100389 all from NMVPL252.

DIAGNOSIS. C10, C12 and C14 larger than adjacent proximal and distal plates. Proximal half of C16 and C18 narrower than distal half. C17 not in contact with either proximal angle of C12 or distal angle of C21. A larger than LOP or MOP. Strongly arcuate or geniculate suture between A and C. Distal portion of appendage not differentiated. Styloid large and robust. Proximal ossicular blades strongly recurved. Paired plates distally in appendage without tubercles. Left spine robust, cigar-shaped, >1/2 as long as body, with lateral cutting edge; right spine more slender, sigmoid to geniculate, without cutting edges.

DESCRIPTION. EXTERNAL. *Measurements*. Holotype: body c.28mm long, 15mm wide. Smallest specimen (Figs 1C, 4D): body c.21mm long, 15mm wide. Largest specimen (Fig. 1E): body c.30mm long, 17mm wide.

Plano-concave surface. Plano-concave surface subrectangular, slightly wider than convex surface, with sharp lateral margins of 11 marginal and 2 subcentral plates (Figs 1A-E, 2C-E, 3D-E, 12A), with maximum width at or slightly proximal to latero-distal angles of PLM. PM flat, almost as wide proximally as distally, with convex lateral margins except for abrupt curve before joining proximal margin. Curvature of distal margin of left PM usually higher than that of right PM (Figs 1A-E, 2A,C-E, 3D-E, 5D, 6E, 12A). PLM, ILM and DLM with flat horizontal projections; well-developed, subvertical projections with gently convex cross-section and meeting plano-concave surface at 60° (Fig. 12D-E). PLM more than twice as wide distally as proximally, with subvertical projection subtrapezoidal, of uniform depth in distal 1/3, decreasing in depth proximally (Figs 1A-B, 2A, C-E, 3D, 4B, F, 5A-C, 12B). ILM trapezoidal, slightly shorter than PLM, with distally diverging, gently concave medial margins; subvertical projection subrectangular, comparable in size with those of DLM and PLM, with sutural margin in 2 shallow embayments of about same size. DLM irregularly pentagonal, with convex medial margins, with longer less convex lateral margins, with medial 2/3 of distal margin thickened and slightly domed. Subvertical projections subpentagonal, with sutural margin in 2 embayments. Distal surface of DLM vertical or sloping distally towards convex surface, subtriangular, shallower peripherally, with subcentral vertically elongate narrow toroidal process for spine insertion sitting on

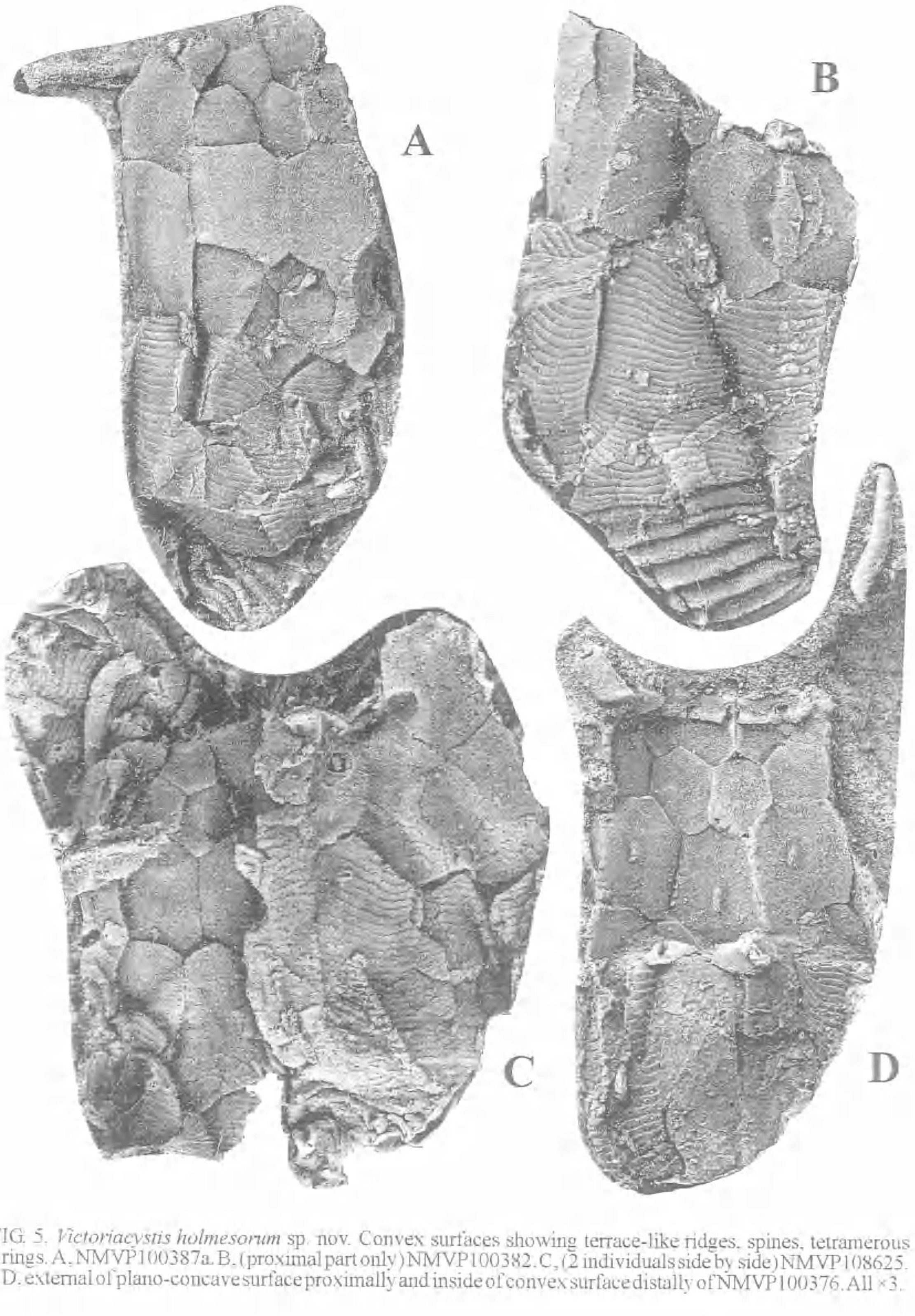

FIG. 5. *Victoriacystis holmesorum* sp. nov. Convex surfaces showing terrace-like ridges, spines, tetramerous rings. A, NMVP100387a. B, (proximal part only) NMVP100382. C, (2 individuals side by side) NMVP108625. D, external of plano-concave surface proximally and inside of convex surface distally of NMVP100376. All ×3.

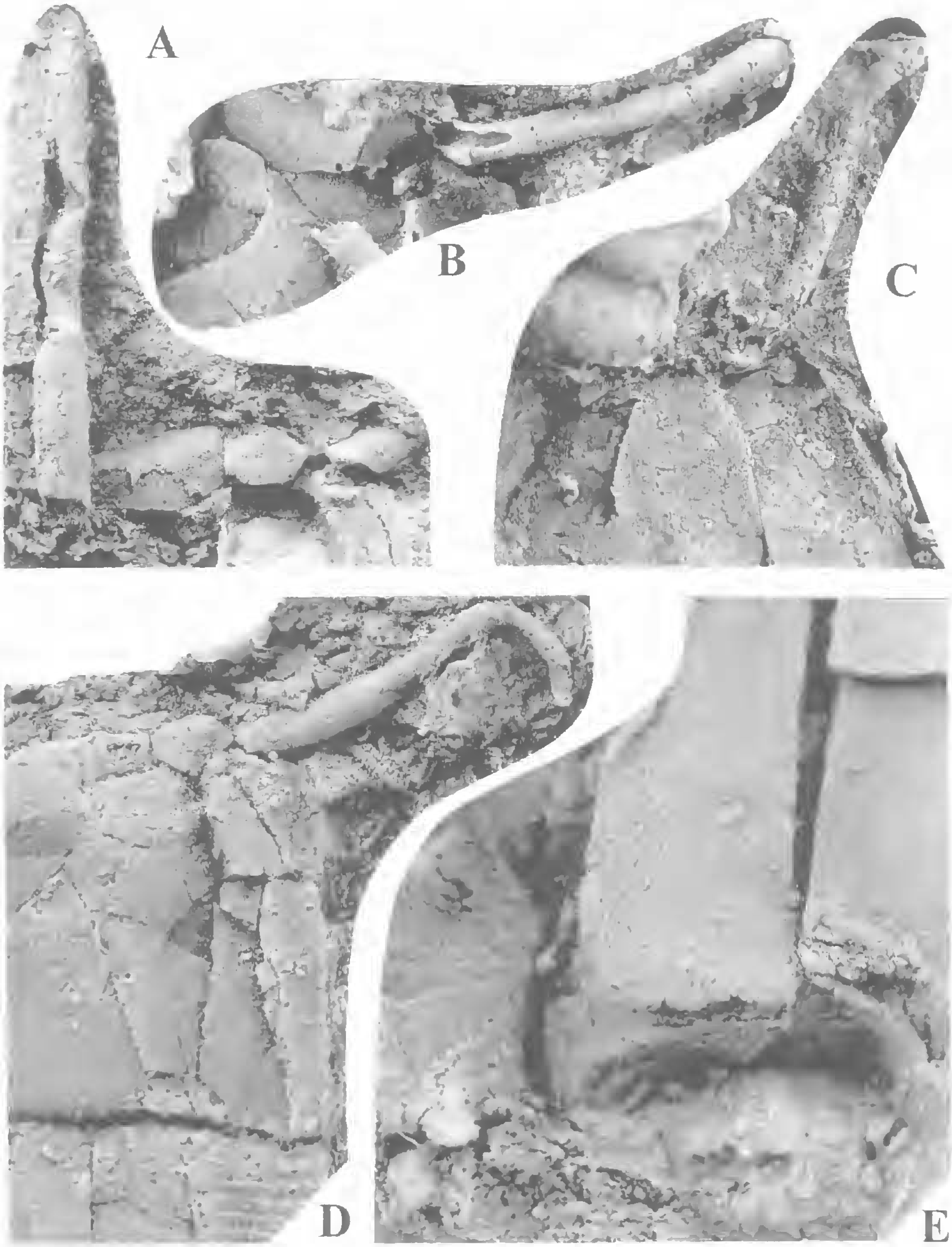

FIG. 6. *Victoriacystis holmesorum* sp. nov. Spines (A-D), plano-concave surface (C,D) and proximal body excavation (E). A, left spine NMVP100367, ×5. B, right spine NMVP100374, ×5. C, right spine NMVP100384, ×5. D, right spine NMVP100361, ×5. E, NMVP100370, ×7.

slightly raised, lens-shaped projection. Small gap between lateral margin of each LOP and medio-distal margin of each DLM (Figs 1A-B, 2A,C, 3D, 4A-B,F, 5A, 11A, 12A). MOP and LOP forming almost transverse row along distal margin. Vertical projections about 1/3 as large as horizontal projections. MOP about twice as wide as each LOP, rectangular, with straight distal margin. LOP c.3/5 size of DLM, subpentagonal, with blunt round latero-distal angles (Figs 1A-D, 2C-D, 6A-B,D, 7A, 12A). Plate A generally subpentagonal to shield-shaped, c.1.5 times as large as each DLM, wedged between left 1LM and C, with medial margin arcuate or geniculate, with lateral margin twice as long as latero-distal margin. Plate C largest plate in body, c.1/2 as long and wide as plano-concave surface, with medio-distal margin almost 1.5 times as long as latero-distal margin. Small, round tubercles subcentrally on A and on distal 1/3 of C (Figs 1A,D, 2C, 3D, 6B,D, 7A).

Convex surface. 20 plates in 5 transverse rows. Rows II-V gently concave distally. Rows I and IV with 5 plates each. Rows III and V with 3 plates each. Row II with 4 plates (Figs 4A-F, 5A-C, 12C). Maximum convexity c.2/3 of way proximally along C20 and C22 (Fig. 12B). Plates generally decreasing in size distally, except C15 and C19, which are smaller than C10 and C14. C2-C4 subpentagonal, subequal, larger than subrectangular C1 and C5 and just smaller than hexagonal C7 and C8. Distal margins of C1-C5 broadly convex. Lateral margins of C3 usually concave, sometimes straight (Figs 4A-F, 5A,C, 12C). Proximo-medial and proximo-lateral margins of C7 and C8 and proximal margins of C6 and C9 convex. C6 and C9 subpentagonal, often more expanded transversely than proximo-distally (unlike C2-C4), with subparallel laterally diverging (rarely converging) proximal and distal margins (Figs 4A-F, 5A,C, 12C). C10 and C14 wider than long, subhexagonal, with very short medio-distal and medio-proximal margins. C12 hexagonal, slightly wider proximally than distally (Figs 4A-F, 5A-C, 12C). C15 and C19 subtrapezoidal, with convex margins, much wider distally than proximally (Figs 4A-C, D-E, 5A-C, 12C). C16 and C18 with lateral margins strongly diverging proximally, with latero-distal margins 1/2-1/3 length of medio-distal margins. Suture between C16 and C18 extremely short distally, slightly longer in proximal section. C17 subrounded to subelliptical, <1/2 as long as C16 and C18, never in contact with C12 or C21, flat or slightly raised above convex surface (Figs 4A-C,E-F, 5A- C, 8D, 12C). C21 shield-shaped, subhexagonal, with gently convex or rarely straight latero-distal margins meeting at obtuse angle, with proximo-lateral margins straight in distal 1/2 and convex in proximal 1/2 (Figs 4A-F, 5A-C, 8D, 10C, 12C). C20 and C22 largest plates on convex surface, almost twice as long as wide, with oblique distal margins, with convexity of lateral margins increasing slightly proximally (Figs 4A-C,E-F, 5A-C, 7B, 10C, 12C).

Sculpture. Terrace-like ridges on PLM (Figs 1A-E, 2A, C-E, 3D-E, 5D, 11C, 12A) and C20-C22 (Figs 4A-F, 5A-C, 8D, 10C, 12A-C), transverse, mostly uniform distance apart, never anastomosing, interrupted abruptly at interplate sutures. Ridges near proximo-lateral angles of PLM, C20 and C22 and near proximal margins of C20 and C22 usually short, interrupted medially, sometimes bifurcating, more crowded together than elsewhere. Bifurcations of ridges rare, in either direction. Ridges on PLM more robust than on C20-C22, with slightly deeper and steeper proximal slope, with distal slope almost flat, slightly convex proximally and gently concave distally. Ridges on C21 variable, with 5-6 most proximal ridges rarely transverse (Fig. 5B), more often convex distally (Figs 4A-C, 8D), with convexity decreasing in straighter more distal ridges, with subcentral ridges straight or chevron-shaped with apex of chevron pointing proximally, with lateral 1/2 of chevron arms transverse or slightly diverging distally, with most distal ridges transverse.

Body stereom. Uniformly compact (Fig. 6E) or of minute perforations with irregular outline and no evident distribution pattern (Fig. 8D). Perforations absent or very small along plate margins, frequently replaced by narrow band of short close spaced straight striations. Stereom of centre of plates rarely coarser than peripheral stereom, with more widely spaced larger pores and thicker trabeculae especially on MOP, LOP, A and C (Fig. 1A,D). Stereom of terrace-like ridges on convex surface granular, more compact at free margins. Stereom of ridges on plano-concave surface compact along free margins, coarse and irregularly perforated by small pores on distal 1/2, giving rise to faint striations on proximal 1/2. Striations at c.45° in medio-lateral direction.

Spines. Left spine straight, massive, 1/2-5/8 body length, cigar-shaped, tapering to a blunt end in distal 1/3, with cross-section of proximal 2/3 asymmetrical, with semicircular medial margin,

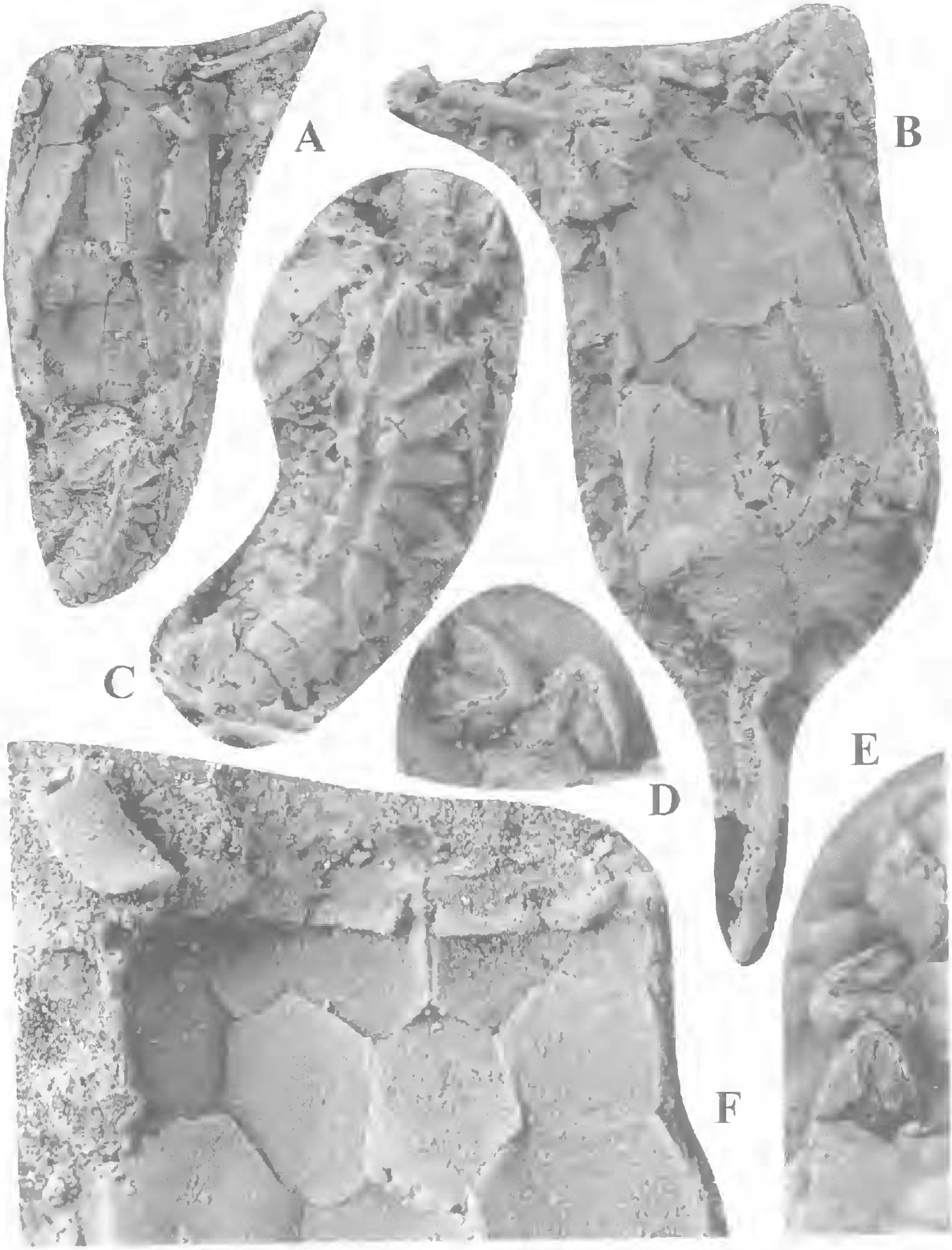

FIG. 7. *Victoriacystis holmesorum* sp. nov. A, plano-concave surface partly disarticulated and with spine; C, detail of proximal appendage of NMVP100374, ×2 and ×5, respectively. B, inside of plano-concave surface of NMVP100371, ×3. D,F, proximal and distal articular surfaces of ossicles NMVP108627, ×10. E, inside of distal part of convex surface of NMVP100376, ×7.

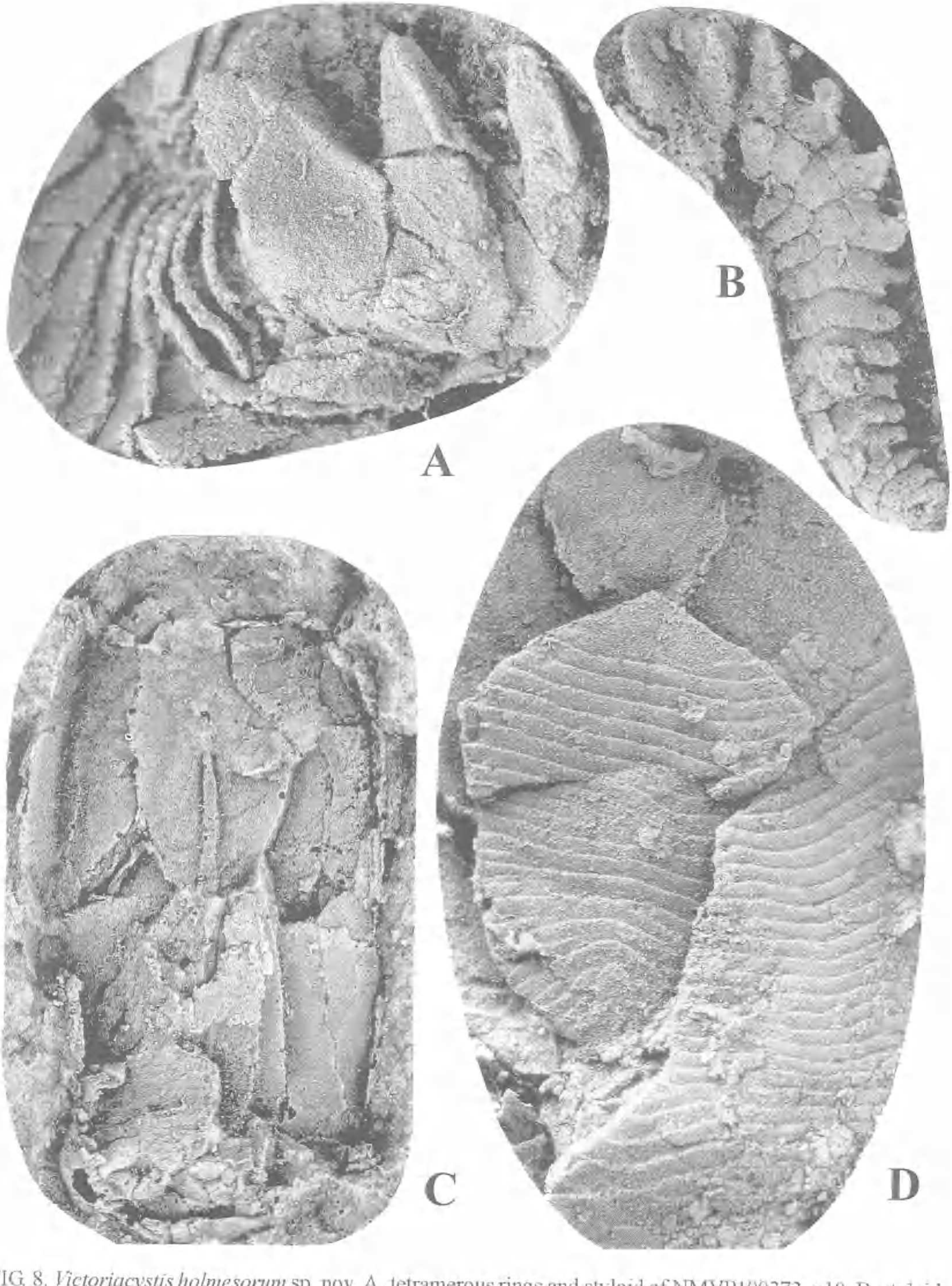

FIG. 8. *Victoriacystis holmesorum* sp. nov. A, tetramerous rings and styloid of NMVP100373, ×10. B, styloid, ossicles and paired plates of appendage of NMVP100363 (holotype), ×5. C, inside of plano-concave surface of NMVP100369, ×3. D, proximal surface ornament of NMVP100370, ×7.

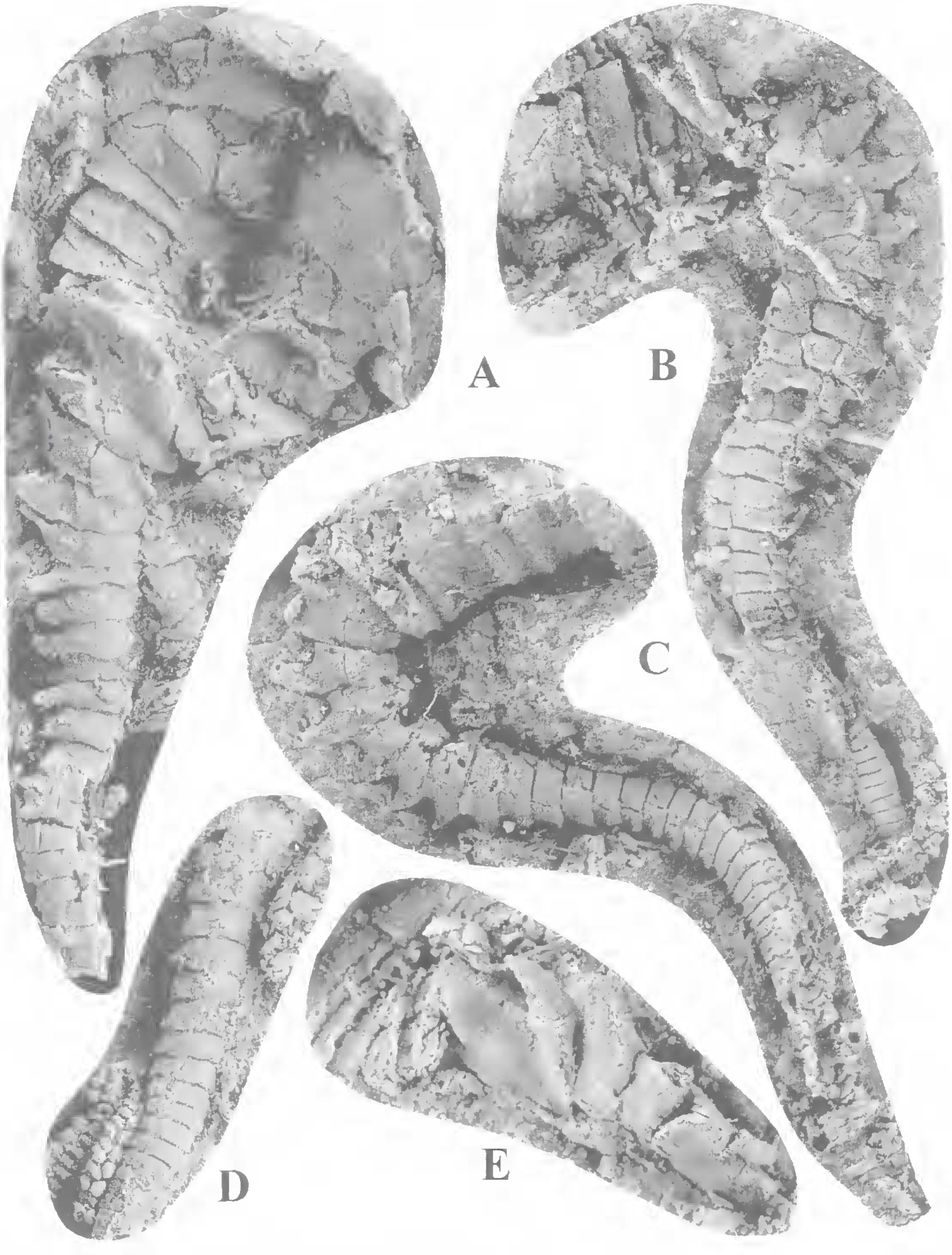

FIG. 9. *Victoriacystis holmesorum* sp. nov. Tetramerous rings, styloid, ossicles and paired plates. A, NMVP100378b, ×5. B,C, NMVP100366, ×3. D, NMVP100364, ×5. E, NMVP100387b, ×7.

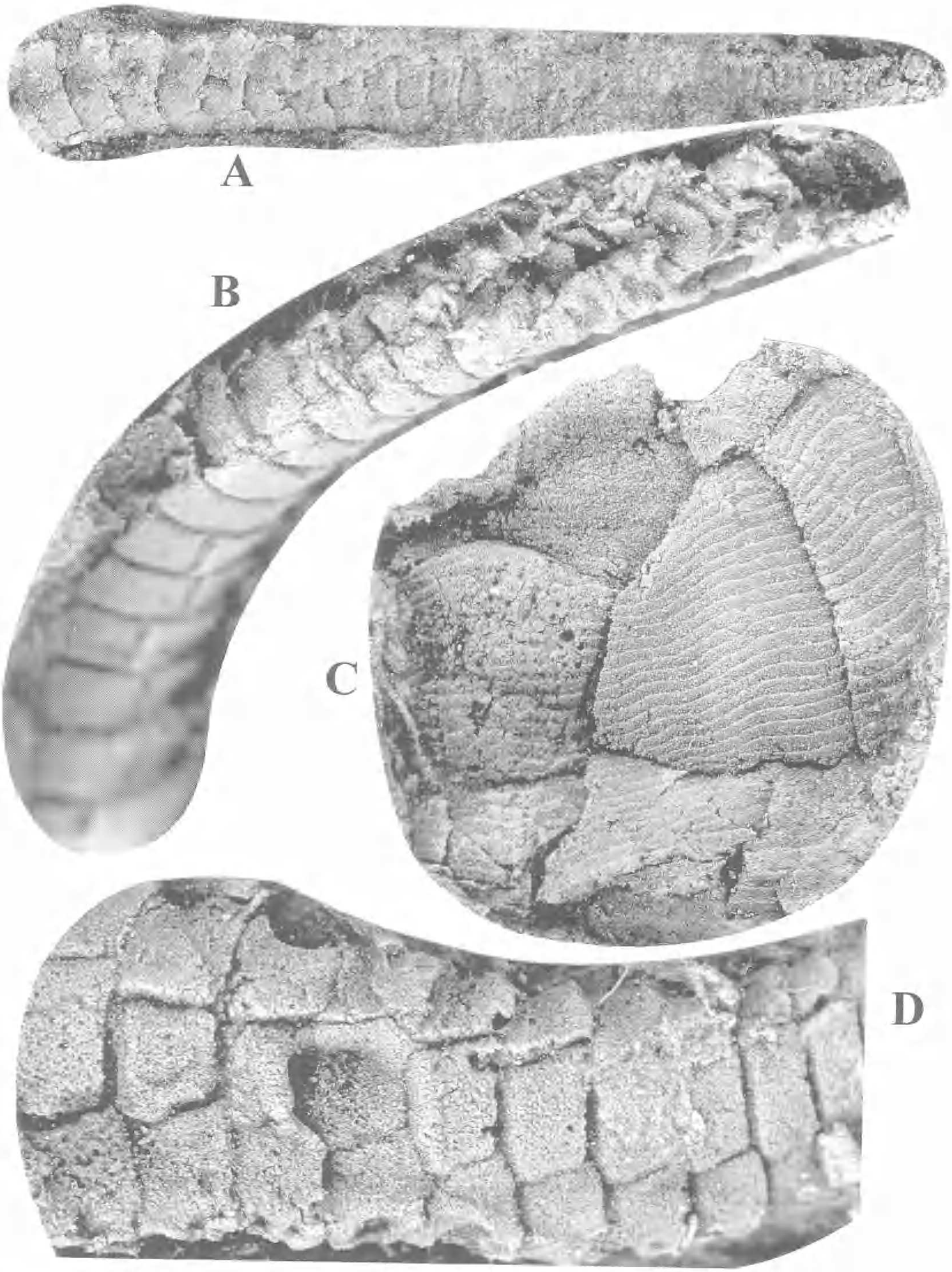

FIG. 10. *Victoriacystis holmesorum* sp. nov. Convex surface (C), terrace-like ridges (C), ossicles and plates (A,B,D). A,C, NMVP100389, ×6. B,D, NMVP100366, ×15.

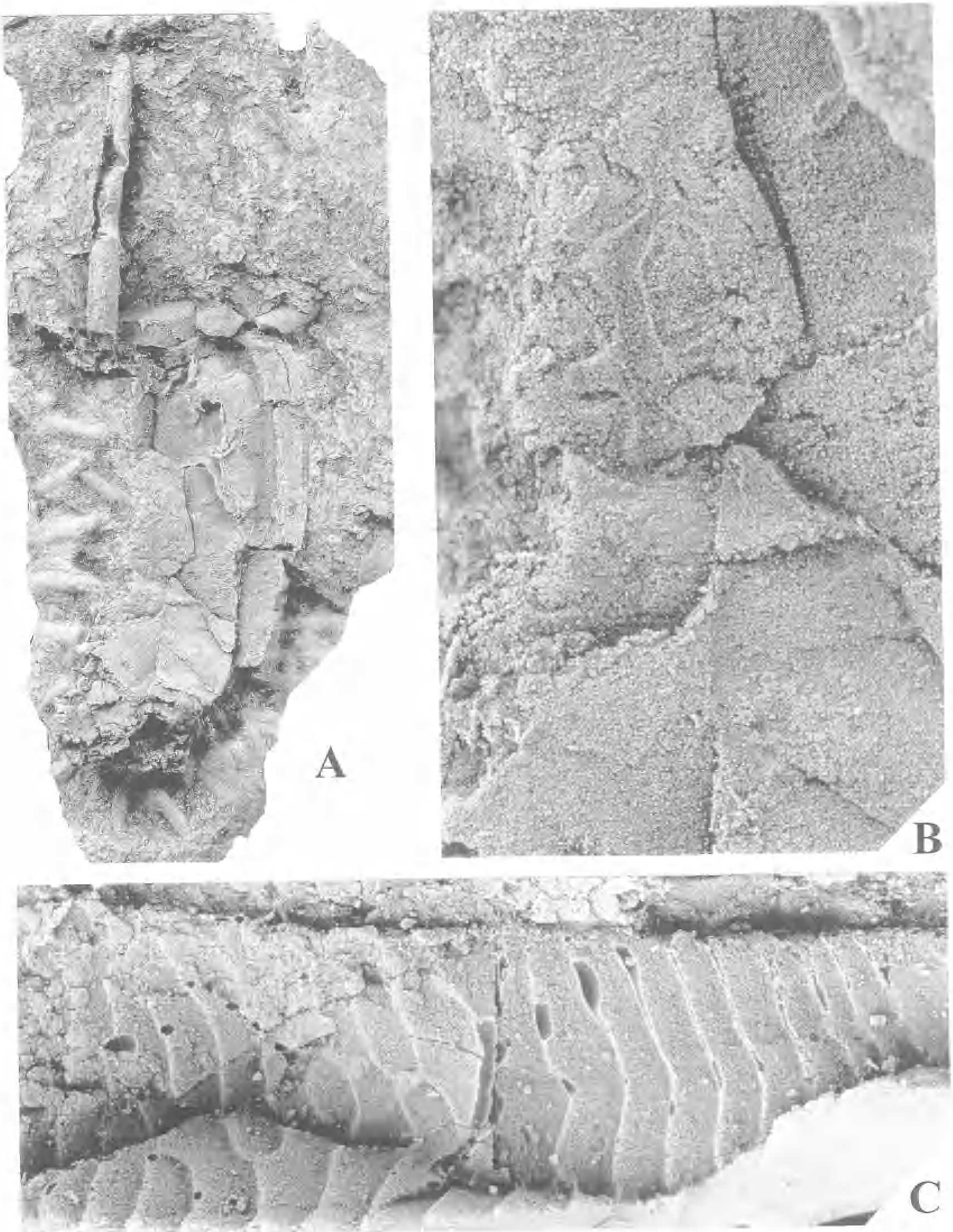

FIG. 11. *Victoriacystis holmesorum* sp. nov. Internal side of central part of convex surface (A,B) and transverse section of terrace-like ridges of plano-concave surface (C). A,B, NMVP100367, ×3 and ×12, respectively. C, NMVP108627, ×10.

with sharp lateral margin becoming more indistinct distally, with distal 1/3 circular or broadly elliptical in section (Figs 3A, 4A, 6A, 11A), with oblique gently convex, surrounded medially by slightly thickened margin and carrying low conical subcentral projection, giving insertion to toroidal process (Figs 2E, 3A, 5D, 6A, 7E). Right spines described individually: some (Fig. 3B-C) more slender, slightly shorter than left spine, uniformly decreasing in diameter proximo-distally, slightly flattened in proximal 1/2, with weak lateral keel, with proximal 1/4 separated from rest of the spine by abrupt geniculation; with distal 3/4 of spine straight or very gently curved medially; most others gently (Figs 2D-E, 3D-E, 5A-D, 6B-C, 7A-B) to strongly convex laterally (Figs 1A, 5C, 6D) proximally, laterally concave distally, forming a distinct distal hook in one specimen, with almost uniform cross-section proximo-distally and with blunt distal end, with articular surface similar to that of left spine, but perpendicular to main axis and without thickened medial margin.

INTERNAL. *Plano-concave surface*. Slightly oblique septum along left 1/2 of inside of C and of left PM, slightly sinuous in its distal 1/2, ending in poorly defined spur-like process subcentrally on distal 1/3 of C, with proximal part of septum convex laterally. Proximo-distally elongate, trough-like area of inside of left PM between septum and lateral margin of left PM. Faint ridge diverging laterally from the spur-like process, running on inside of C and right PM, flanking the lateral margin of the latter. Transverse ridge near distal margins of A and C, slightly concave distally, more robust on A, occupying almost the entire width of A, interrupted laterally on C. Proximal and distal surfaces of ridge sloping gently. Inside of other plates poorly preserved but apparently smooth.

Convex surface. Internal surface of C1-C5 margins slightly thickened (Fig. 5D), surrounded by very shallow peripheral groove, with distal 1/3 (Figs 5D, 7E) occupied by proximally recumbent walls at c.20° to internal surface of plates, extending almost completely across their width. Distal surfaces of transverse walls merging gradually into distal 1/3 of internal side of plates, also slightly raised with respect to their proximal 2/3. Walls on C1 and C5 c.1/2 as wide as walls on C2-C4, slightly thicker than these, torus-shaped with strongly convex, blunt free margin. Walls on C2-C4 rectangular, with straight, thinner free margin and with clear-cut separation of lateral margins from inside of plates. Internal surface of C6-C9 smooth and featureless. Subcentral, proximo-distally elongate thickening on internal surface of C10, C12 and C14. Lateral surfaces of thickenings almost vertical. Thickenings on C10 and C14 roughly elliptical, c. twice as long as wide. Thickening on C12 almost 3 times longer than wide, with subparallel lateral margins. Similar thickening, spindle-shaped in outline and with greater axis at c.60° to body axis, visible in the middle of plate C15 in NMVP100367 (Fig. 11A-B).

Internal surface of C16 (Fig. 11A-B). Distal 1/2 not clear. Proximal 1/2 with a shallow cruciform area with irregular arms, outlined by thin ridges. Proximal arm short and stout, with gently concave margins, reaching proximo-lateral margin of C16. Distal margin of lateral arm curving distally as sinuous ridge joining lateral margin of distal arm of cross. Distal arm about twice as long as lateral and proximal arms.

APPENDAGE. 1-1.25 times body length; proximal part 3 times wider at proximal ring than at distal ring, with segments of proximal 1/3 of distal part decreasing in size and changing shape distally. Segments of central 1/3 of distal part decreasing uniformly in size and displaying less remarkable changes in shape. Distally appendage whip-like, with segments of approximately constant proportions.

Proximal part. Tetramerous rings with proximal one largest, with remainder of subequal length but decreasing width. Paired ring plates on plano-concave side, slightly smaller than those lying on opposite side, less convex in cross-section, with narrower thickening along distal margins (Figs 1A-B,E, 2A,D-E, 3D, 4A-B,F, 5B, 7B, 8A, 9A-C,E, 12A-C). Distal margin of proximal ring straight, without tubercles. Distal margins of other rings concave, with regularly spaced, subconical to hemispherical tubercles (Figs 1E, 2C-D, 3D, 4A-C, F, 5A-B, 8A, 9A-C,E). Articular surfaces on lateral ends of ring plates on same side as convex surface, proximo-distally elongate, triangular, with a subcentral, roughly circular shallow area (Figs 1B,E, 2C-D, 8A, 9A).

Intermediate part. Styloid (Figs 1B,E, 2D, 4B,F, 7A,C, 8A,B, 9A,E, 12A-B, 13B) robust. Proximal articular process just beneath proximal blade, subhorizontal, flattened, subtriangular. Proximal blade expanded transversely, recumbent, with free margin blunt, semicircular to broadly semielliptical. Narrow, sharp, median

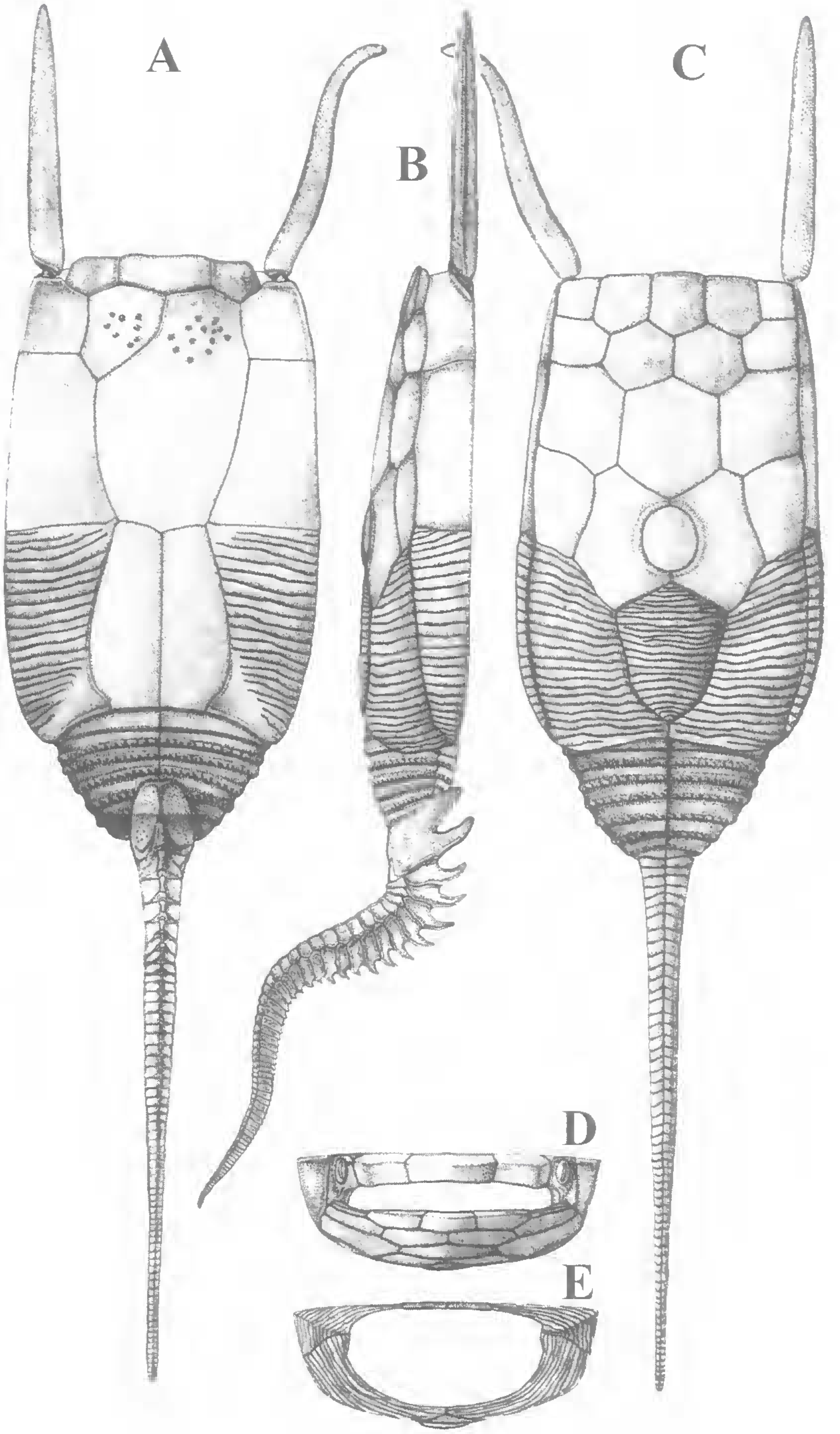

FIG. 12. Reconstruction of *Victoriacystis holmesorum* sp. nov. A, plano-concave surface. B, left lateral view. C, convex surface. D, distal surface (distally articulated spines omitted). E, proximal surface (appendage omitted).

longitudinal keel ending abruptly before reaching free margin of proximal blade and widening slightly in its distal 1/2. Region of blade facing proximally between free margin and insertion of proximal articular process vaulted. Distal blade 3 times as high as wide, spike-like. Proximal margin of distal blade narrowly acute but not sharp, slightly concave in lateral view in its lower 2/3 and almost straight in its upper 1/3 before merging into blunt blade apex. Lateral surfaces of distal blade flat to very gently concave in upper 2/3.

Distal part. (Figs 2B,D, 4B,F, 7A-C, 8B, 9A-E, 10A-B,D, 12A-C, 13A,C-D). Ossicles of first 5-6 segments slightly more than 3 times as high as long and divided into massive body and blade-like process, or apex. Processes of first 3 or 4 ossicles (Fig. 13A) almost as high as their bodies, gradually decreasing in height and length distally, wedge-shaped in transverse section, with strongly curved proximal margin. Proximal margins of processes merging into sharp median longitudinal keel with asymmetrical parabolic profile and occupying proximal 1/3 (in first 3 ossicles) to 1/2 (in subsequent 2 or 3 ossicles) of ossicular length. Articular margins for insertion of paired plates bearing smaller, shallower proximal facet and larger, deeper distal facet. Ossicles 7-9 (Fig. 10D) 3 times as high as long; processes narrower than on more proximal ossicles, decreasing in size distally, confined to distal 1/3-1/4 of ossicular length, subtriangular in lateral view. Keel slightly concave to straight in lateral view. Remaining ossicles (Figs 9B-D, 10A-B) subrectangular in lateral view, 3 times as high as long, with almost straight proximal and distal margins; processes diminishing distally, cuspate, shaped like an equilateral triangle in cross-section. Terminal ossicles without processes.

Proximal (Fig. 13C) and distal (Fig. 13D) articular surfaces parabolic, slightly taller than wide, comprising an outer interossicular depression, an inner interossicular depression and a median interossicular groove. Outer interossicular depression delimited laterally by slightly thickened ossicular margin of uniform width and medially by thinner, ascending ridges forming external subelliptical boundary of inner interossicular depression, becoming thinner and narrower apically. Inner interossicular depression elliptical, occupying most of apical 2/3 of articular surface. Internal boundary of depression delimited by faint vertical ridges flanking median interossicular groove. Abapical ends of ascending ridges turned abruptly laterally, merging into free, semicircular rims of 2 articulation bosses on proximal articular surface of ossicle. Ridges marking proximal margins of subtriangular facets for articulation with paired plates of preceding segment of distal part of appendage.

Distal articular surface of ossicles (Fig. 13D) differing from proximal articular surface in apically tapering median interossicular groove, comparatively deeper lateral regions of outer ossicular depression and trough-like, elongate articular pit delimited by 2 thick ridges diverging apically and laterally, occupying same position as articular bosses on outer ossicular depression.

Paired plates of distal part of appendage changing shape and size throughout appendage length (Figs 2D, 4B,F, 8B, 9A-C, 10A-B,D). Each plate articulating with distal facet of overlying ossicle and with proximal facet of next distal ossicle. First 4 pairs of plates at least twice as high as long, with gently convex distal margin, with sinuous to straight proximal margin. Subsequent 4 pairs of plates with decreasing height/length ratio almost as long as high. Remaining plates subsemicircular in lateral profile.

Appendage stereom. Stereom of proximal rings generally compact, especially along free margins of ring plates, or with small subcircular pores, resembling that of central surface area of body plates, often with small granulations distributed randomly, rarely with coarse trabeculae and irregular pores. Styloid stereom usually compact, rarely microperforate, sometimes with irregular, elongate trabeculae near margins of lateral surfaces of distal blade. External surface of plates and ossicles of distal part of appendage usually covered with regular, subcircular shallow pits separated by short trabeculae. Stereom near free margins of ossicles and plates generally more compact, with smaller pits and more irregular trabeculae, the latter sometimes elongate and giving rise to faint striations, especially near apex of ossicular processes.

DISCUSSION. *Victoriacystis holmesorum* closely resembles *V. wilkinsi* and *Rhenocystis latipedunculata* Dehm, 1932 especially in the number and arrangement of plates on the convex surface (Ruta, 1997, in press; Ruta & Bartels, 1998). *Rhenocystis* is distinguished from *Victoriacystis* by the plate arrangement of row II, in which C7 and C8 are separated by interposition of C3 and C12. *V. holmesorum* is larger and more robust than *V. wilkinsi* and *R. latipedunculata*. It

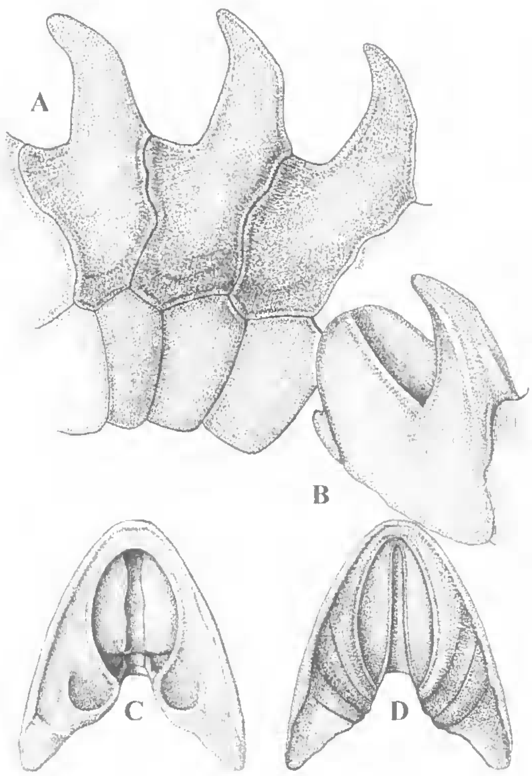

FIG. 13. Reconstruction of *Victoriacystis holmesorum* sp. nov. A, most proximal segments of distal part of appendage. B, styloid in left laterodistal view. C,D, proximal and distal articular surfaces of ossicle of intermediate region of distal part of appendage.

differs from *V. wilkinsi* in its differentiated distal part of the appendage, larger plates of row III, C10 C12 and C14, with respect to more proximal and distal elements, narrower proximal 1/2 of C16 and C18 with respect to distal 1/2, lack of contact between C17 and either proximal angle of C12 or distal angle of C21, larger A with respect to LOP and MOP, usually strongly arcuate or geniculate suture between A and C, more robust and larger styloid, more strongly recurved proximal ossicular blades, absence of tubercles from the paired plates of the distal part of the appendage and longer and more robust spines, sometimes with remarkably different morphology.

Pseudovictoriacystis gen. nov.

TYPE SPECIES. *Pseudovictoriacystis problematica* sp. nov.

ETYMOLOGY. Greek *pseudo*, false, plus *Victoriacystis*; alluding to resemblance between new genus and *Victoriacystis*. Feminine.

DIAGNOSIS. Distal 1/2 of convex surface of rows I and III, with 5 and 3 elements respectively. Distal margin of convex surface slightly convex centrally, concave laterally. C12 in contact with C2-C4. Lateral margins of C12 diverging slightly distally. C10 and C14 larger than C12, sutured with C1-C2 and with C4-C5, respectively. Proximal 1/2 of convex surface of rows IV and V, the former including C15, C17 and C19. C15 and C19 subtrapezoidal, their lateral margins 1.5 times as long as medial margins. C17 shield-shaped, at least 3 times as wide distally as proximally, with 3-lobed distal margin. C20 and C22 almost 1/2 as long as body, with strongly sinuous medial margins and very gently convex lateral margins. C21 narrowly inserted between C20 and C22, at least twice as long as wide, reaching maximum width in proximal 1/3.

Pseudovictoriacystis problematica sp. nov.
(Figs 14-16)

ETYMOLOGY. Greek *problema*, question; alluding to the puzzling plate configuration of the convex surface.

MATERIAL. HOLOTYPE: NMVP100383 from NMVPL252.

DIAGNOSIS. As for genus.

DESCRIPTION. Length 24mm, width 16mm, broadly rectangular. DLM and LOP of left side, C15, spines and articulated appendage not preserved.

Plano-concave surface. Plating pattern and general plate proportions similar to *Victoriacystis holmesorum*. Differences as follows (Figs 14A, 15A): maximum body width about halfway along PLM; lateral margins of ILM and DLM straight; shallower lateral body walls; much greater PLM/ILM length ratio; length of distal margin of PLM/length of proximal margin of PLM slightly lower; proximal 1/3 of lateral margins of PLM more strongly curved medially; distal margins of PLM sinuous, with medial 1/2 proximally convex and lateral 1/2 proximally concave; PM about as long as C; lateral margins of PM more gently convex and with most proximal part forming deep semicircular notch; proximo-lateral angles of PM extended as narrow lateral elongate processes; proximal margins of PLM and PM at obtuse angle rather than merging gradually; medial margins of ILM slightly more concave; DLM about twice as long as wide, with

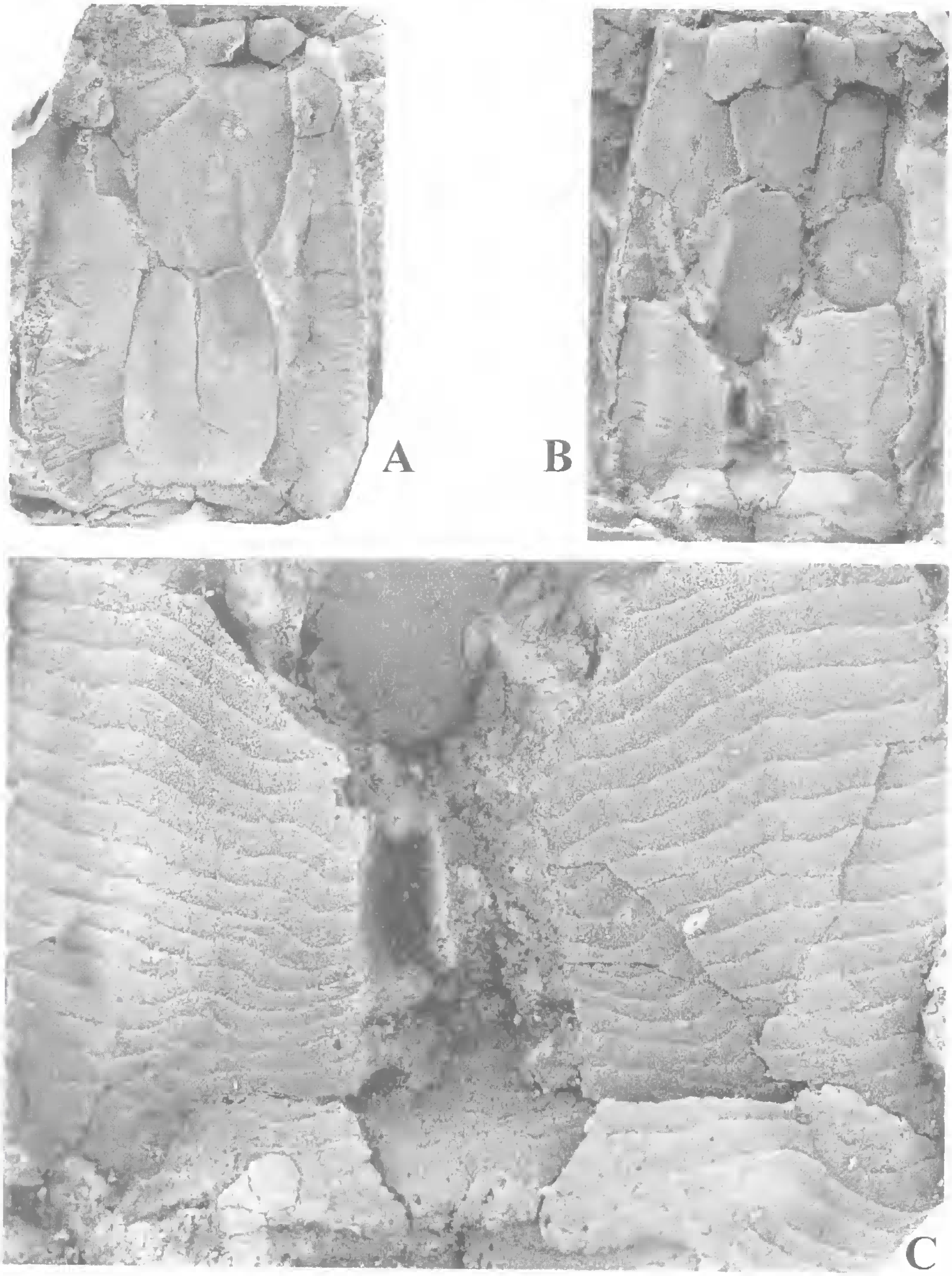

FIG. 14. *Pseudovictoriacystis problematica* gen. et sp. nov. Holotype, NMVP100383. A,B, plano-concave and convex surfaces, respectively, ×3. C, close-up of C20-C22, ×10.

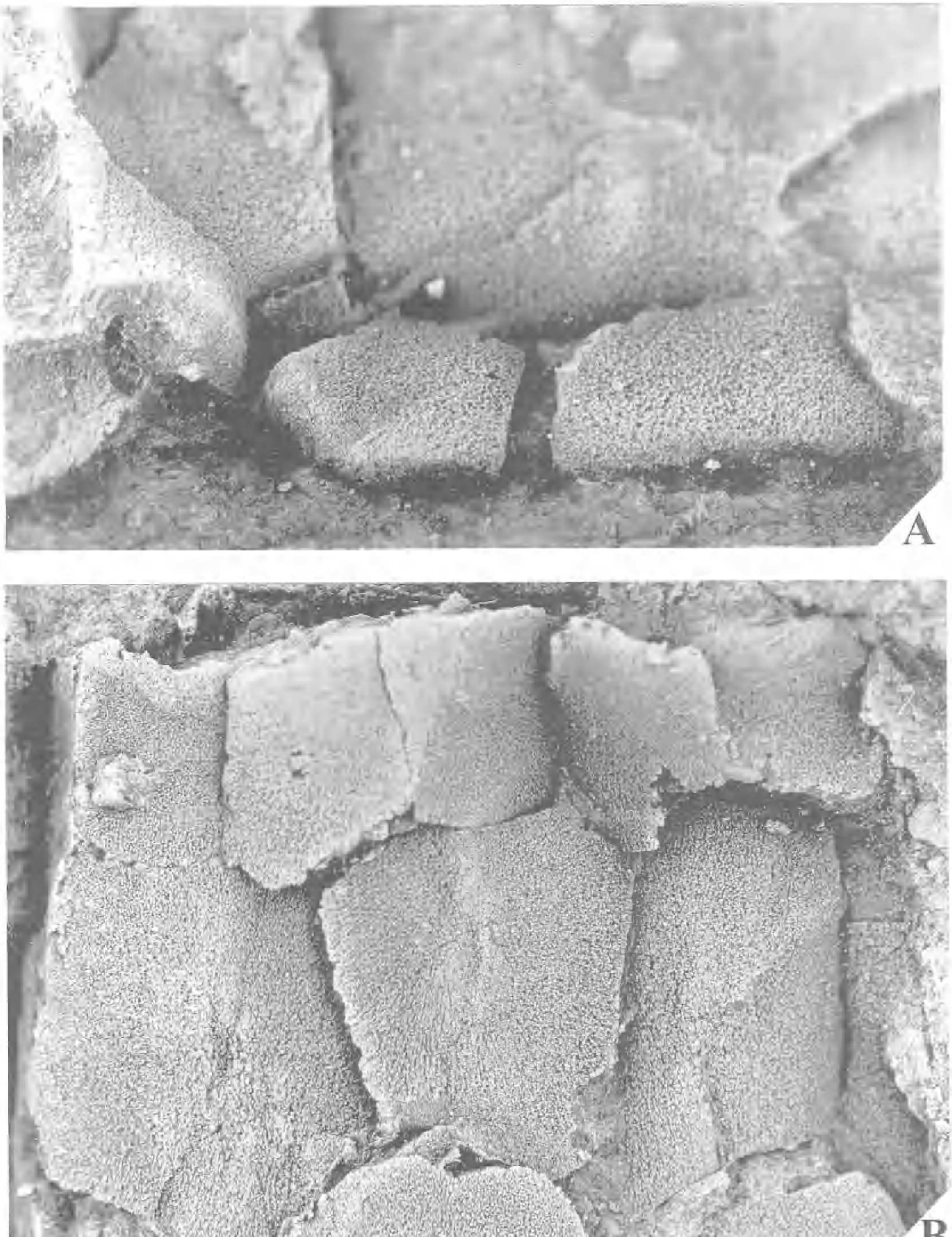

FIG. 15. *Pseudovictoriacystis problematica* gen. et sp. nov. Holotype, NMVP100383. A, close-up of right LOP, MOP and articular surface of right DLM, ×15. B, close-up of distal part of convex surface, ×10.

distally protruding articular region for spine insertion and shallow depressed area medial to articular region; distal surface of articular region teardrop-shaped, with lateral end forming an acute angle and divided into 2 distinct parts; lateral part broadly triangular and shallowly concave; medial part subcircular and markedly convex distally, bearing small, subcentral toroidal process giving rise to a short, faint medial and lateral ridge; suture between A and C mostly straight, at c.60° to longitudinal body axis, gently curved and meeting proximal margin of MOP in distal 1/4.

Convex surface (Figs 14B-C, 15B, 16). Slightly disrupted; proximal 1/2 reconstructed tentatively. Transverse rows of plates 4; distal row with 5 plates, homologous with C1-C5 of other anomalocystitids (e.g. *Rhenocystis* and *Victoriacystis*). C2 and C4 subtrapezoidal, with distally converging lateral and medial margins and with lateral 2/3 of proximal margins broadly convex and lying proximal to proximal margin of C3. C1 and C5 subrectangular, about twice as long as wide, with broadly concave distal margins. Row II of 3 plates (=C10, C12 and C14 based on shape and proportions). C10 and C14 longer than wide, subpentagonal, with medial angles strongly developed into points. C12 in contact with C3 medially and C2 and C4 laterally. Lateral margins of C12 mostly straight, slightly convex at proximal and distal ends. C15 and C19 smaller, subtrapezoidal, with convex margins. C17 with L/W ratio of 1.4, with lateral margins divided into sinuous distal 1/2 and distally diverging concave proximal 1/2, with distal margin broadly convex, with expanded central section. C20 and C22 with distal to proximal margins: distal margins <1/3 plate length, oriented slightly oblique to longitudinal axis, slightly concave; lateral margins very gently convex in distal 1/2, more strongly convex in proximal 1/2. Proximal margins merging into lateral margins, forming proximally protruding blunt-ended angles, with lateral 2/3 of proximal margins slightly convex, with medial 1/3 gently sinuous, forming central excavation into proximal margin. Medial margins convex but with smooth invagination distal to rounded medial projections at proximal end. C21 (Fig. 14B-C) trapezoidal, inserted between C20 and C22, with gently convex proximal margin, with 4-5 irregular ridges, with one bifurcated laterally.

Sculpture. PLM with robust terrace-like ridges, with thickened free margin; ridges irregularly sinuous, unevenly spaced, sometimes interrupted medially or giving rise to irregular lateral bifurcations, with most proximal ridges short and at c.45° to body axis, with smooth broadly trapezoidal area of external surface (Fig. 14A). Terrace-like ridges on C20 and C22 (Figs 14B-C) less steep than on PLM, without thickened free margin, oriented mainly transverse to longitudinal body axis but irregularly sinuous. Single, sigmoidal ridge at 45° to longitudinal axis on proximolateral 1/4 of external surface of C19.

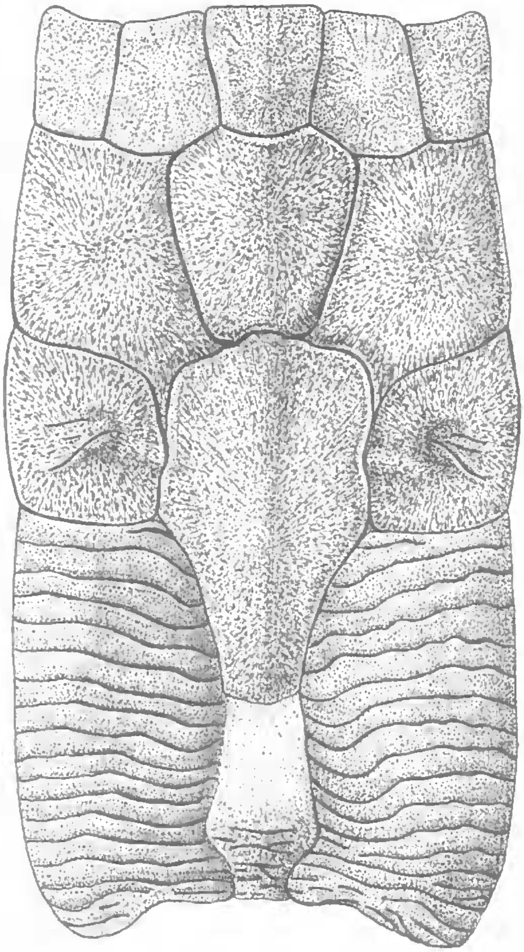

FIG. 16. Reconstruction of convex surface of *Pseudovictoriacystis problematica* gen. et sp. nov.

Body stereom. Stereom of plano-concave surface similar to that of *Victoriacystis holmesorum*, but consisting of slightly coarser meshwork, especially in the centres of the plates, often forming a reticulate pattern of irregular pores and trabeculae. Peripheral surface, especially on A, C, MOP and ILM, with elongate pores and thin, straight trabeculae arranged radially (Figs 14A, 15A). Stereom of convex surface retiform except on C20-C22 (Fig. 15B-C). All other plates, but especially those of the 2 most distal transverse rows, with distinct surface pattern with pores increasing in size, becoming more elongate and arranged more regularly from centre to margins of plates, separated by radiating trabeculae, often dichotomously branching towards the periphery. Pores near plate margins polygonal, separated by short trabeculae, giving rise to coarse, cancellate surface pattern of stereom. Stereom of periphery of C17 and of medial 1/2 of C19 of densely spaced, circular to subelliptical pores, without obvious radiating arrangement of trabeculae.

REMARKS. The possibility that NMVP100383 is a teratological individual of *Victoriacystis holmesorum* cannot be entirely ruled out. It closely resembles the latter in plating of the plano-concave surface. Although rare, pathological mitrate specimens are known (Ruta, 1998). However, in all known cases, abnormal individuals can be assigned to known species, based on their possession of most of the characters shared with normal individuals.

Pending discovery of additional specimens to confirm diagnostic features, NMVP100383 is here placed in a new taxon because the configuration of its convex surface reveals a unique combination of attributes not observed in any other species.

Plate arrangement of distal 1/2 of convex surface resembles that of *Placocystites forbesianus* de Koninck, 1869 (Jefferies & Lewis, 1978) from the English Wenlock. In *Pseudovictoriacystis* and in *Placocystites*, C10, C12 and C14 are sutured with row I, there is no intervening row II and C12 is slightly smaller than both C10 and C14. *Pseudovictoriacystis* differs from *Placocystites* in being much longer than wide, in displaying a more limited distribution of terrace-like ridges, in possessing 5 rather than 3 plates in row I and in showing a much simpler plate configuration on proximal 1/2 of convex surface, apparently without plates C16 and C18 and with enlarged C17. Furthermore, C3 is separated from C10 and C14 by interposition of C2 and C4 and appears to be comparable in size with C1 and C5 and slightly smaller than C2 and C4.

The much older *Kopficystis kirkfieldi* Parsley, 1991 from the Trentonian of Ontario, vaguely resembles *Pseudovictoriacystis* in its 3-plated transverse row on distal 1/2 of convex surface. However, identification of the skeletal plates in that taxon is problematic (Ruta, in press). Unlike *Pseudovictoriacystis*, *Kopficystis* has 5 rather than 4 transverse rows of plates. Assuming the correctness of plate homologies discussed by Parsley (1991) and Ruta (in press), the most distal skeletal elements in this anomalocystitid correspond to C1, C6, C9, C10, C12 and C14 and to CM1, o, j, gl, i and e respectively in the terminology of Parsley (1991).

Although *Pseudovictoriacystis* displays a unique set of skeletal features, it is impossible to ascertain its affinities; we regard this form as deriving from a *Victoriacystis*-like ancestor.

ACKNOWLEDGEMENTS

We thank David Holloway (Museum of Victoria), Steve Eckardt and Frank and Enid Holmes for help in the field. M.R. is grateful to the Queensland Museum (Brisbane) for generous hospitality and for the use of facilities. A.R. Milner (Birkbeck College, University of London), R.P.S. Jefferies, A.C. Milner, S.J. Culver and L.R.M. Cocks (Natural History Museum, London) read a draft of the manuscript. P. Crabb (Natural History Museum, London) photographed the specimens. We thank Dennis Kolata and Colin Sumrall for useful reviews but the views expressed herein are those of the authors alone. This work was carried out while M.R. was in receipt of a European Community grant (Training and Mobility of Researchers).

LITERATURE CITED

CASTER, K.E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology 34: 1-47.

CASTER, K.E. & GILL, E.D. 1967. Family Allanicytidiidae, new family. Pp. S561-S564. In Moore, R.C. (ed.) Treatise on invertebrate paleontology, Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas : New York).

DEHM, R. 1932. Cystoideen aus dem rheinischen Unterdevons. Neues Jahrbuch für Mineralogie, Geologie und Paléontologie. Beilage-Band, Abteilung A 9: 63-93.

GILL, E.D. 1948. A new trilobite from the Yeringian (Lower Devonian) rocks of Kinglake, Victoria. Proceedings of the Royal Society of Victoria 59: 8-19.

GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology 41: 5-71.

HOLLOWAY, D.J. & JELL, P.A. 1983. Silurian and Devonian edrioasteroids from Australia. Journal of Paleontology 57: 1001-1016.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3: 1-128.

JEFFERIES, R.P.S. 1968. The Subphylum Calcichordata (Jefferies 1967) – primitive fossil chordates with echinoderm affinities. Bulletin of the British Museum (Natural History), Geology Series 16: 243-339.

1990. The solute *Dendrocystoides scoticus* from the Upper Ordovician of Scotland and the ancestry of chordates and echinoderms. Palaeontology 33: 631-679.

JEFFERIES, R.P.S. & LEWIS, D.N. 1978. The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. Philosophical Transactions of the Royal Society of London, Series B 282: 205-323.

JELL, P.A. 1983. Early Devonian echinoderms from Victoria (Rhombifera, Blastoidea and Ophiocistioidea). Memoirs of the Association of Australasian Palaeontologists 1: 209-235.

KOLATA, D.R. & JOLLIE, M. 1982. Anomalocystitid mitrates (Stylophora, Echinodermata) from the Champlainian (Middle Ordovician) Guttenberg Formation of the Upper Mississippi Valley Region. Journal of Paleontology 56: 531-565.

KONINCK, M.L. de 1869. Sur quelques échinodermes remarquables des terrains paléozoiques. Bulletin de l'Académie Royale des Sciences Belgique 28: 544-552.

PARSLEY, R.L. 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). Bulletins of American Paleontology 100: 5-57.

RUTA, M. 1997. Redescription of the Australian mitrate *Victoriacystis* with comments on its functional morphology. Alcheringa 21: 81-101.

1998. An abnormal specimen of the Silurian anomalocystitid mitrate *Placocystites forbesianus*. Palaeontology 41: 173-182.

In press. A cladistic analysis of the anomalocystitid mitrates. The Zoological Journal of the Linnean Society.

RUTA, M. & BARTELS, C. 1998. A redescription of the anomalocystitid mitrate *Rhenocystis latipedunculata* from the Lower Devonian of Germany. Palaeontology 41: 771-806.

RUTA, M. & JELL, P. A. 1999a. *Adoketocarpus* gen. nov., a mitrate from the Ludlovian Kilmore Siltstone and Lochkovian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 377-398.

1999b. A note on *Victoriacystis wilkinsi* (Anomalocystitida: Mitrata) from the Upper Silurian of Victoria. Memoirs of the Queensland Museum 43: 423-430.

RUTA, M. & THERON, J.N. 1997. Two Devonian mitrates from South Africa. Palaeontology 40: 201-243.

STRUSZ, D.L. 1972. Correlation of the Lower Devonian rocks of Australasia. Journal of the Geological Society of Australia 18: 427-455.

TALENT, J.A. 1967. Silurian sedimentary petrology and palaeontology. Bulletin of the Geological Survey of Victoria 59: 24-29.

UBAGHS, G. 1967. Stylophora. Pp. 496-565. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York).

1969. Les échinodermes carpoides de l'Ordovicien inférieur de la Montagne Noire (France). Cahiers de Paléontologie. (Éditions du Centre National de la Recherche Scientifique: Paris).

VANDENBERG, A.H.M. 1988. Silurian-Middle Devonian. Pp. 103-146. In Douglas, J.G. & Ferguson, J.A. (eds) Geology of Victoria. (Victorian Division of the Geological Society of Australia: Melbourne).

VANDENBERG, A.H.M, GARRATT, M.J. & SPENCER-JONES, D. 1976. Silurian-Middle Devonian. Special Publications of the Geological Society of Australia 5: 45-76.

WILLIAMS, G.E. 1964. The geology of the Kinglake district, central Victoria. Proceedings of the Royal Society of Victoria 77: 273-328.

WOODS, I.S. & JEFFERIES, R.P.S. 1992. A new stem-group chordate from the Lower Ordovician of South Wales, and the problem of locomotion in boot-shaped cornutes. Palaeontology 35: 1-25.